PALEOECOLOGY AND PREDOMINANCE FACIES OF LATE DEVONIAN FORAMINIFERA IN SUCCESSIONS OF THE CATSKILL DELTA COMPLEX, WESTERN NEW YORK, U.S.A.

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ABSTRACT

Beyond yielding signals of extinction or stressed ecological conditions, modern and ancient foraminiferal assemblages reflect specific marine depositional environments and depths. Foraminiferal predominance facies and benthic foraminiferal depth zonation has been successfully used to identify specific marine environments dating back to the Carboniferous. Using insights from modern equivalents, correlative assemblages allow for paleoecological analysis and insights. Middle to Late Devonian (Frasnian) black and gray shale beds of western New York contain hundreds of diminutive calcareous and agglutinated foraminifera. The genera within these beds are reminiscent of shallow modern predominance facies. These foraminiferal assemblages and their associated predominance facies correlate well with prior lithologic and geochemical investigations that establish this portion of the Appalachian Basin as a deltaic setting but suggest it is likely inner neritic zone. Dominant genera include several species of *Ammobaculites* and *Saccammina* which suggest that paleodepths did not exceed 50 m throughout the Frasnian. Opportunistic genera reflect a muted crisis associated with the *punctata* isotopic event (Rhinestreet Event) and Lower Kellwasser (Pipe Creek) events. While there are definite shifts in the diversity of assemblages between gray and black shale, the foraminiferal type and feeding mode, indicative of depth and oxygen availability respectively, there is little variation between the distinct shale units. No significance was found between total organic carbon and foraminiferal type of feeding mode. Identification at the species level is problematic but assemblages at the genus-level suggest that the depositional environment was stressed. However, the effects of these marine crisis events were not significant for these foraminifera in comparison to those frequently reported; we found no local extinction for foraminifera at least through the lower Hanover Shale, just prior to the Hangenberg marine crisis event, within this deltaic complex of the Appalachian Basin in western New York.

INTRODUCTION

The Devonian Appalachian Basin in the eastern part of North America has one of the most detailed lithostratigraphic frameworks for a Paleozoic foreland system, which has allowed for excellent interpretations of sea-level history and resulting changes in sedimentation (Arthur & Sageman, 2005; Brett et al., 2011; Ver Straeten et al., 2011; He et al., 2019). However, constraining the paleobathymetry of ancient basins through time (e.g., Western Interior Seaway, Black Sea, etc.) has been problematic, and interpreted depth ranges have undergone multiple revisions. The most recent lithologic and geochemical investigations of the paleobathymetry of the Appalachian Basin in western New York during Late Devonian time have reduced prior estimated depths of ~300 m down to ≥75 m (Arthur & Sageman, 2005). The macro-paleontological record within the deltaic complex is superb; though sparse in the Famennian of western New York, it is thoroughly investigated within the prolific beds of the Frasnian (e.g., Sutton et al., 1970; Thayer, 1974; McGhee & Sutton, 1981; Sutton & McGhee, 1985; Over, 1997), and reflects a series of biocrisis events associated with black-shale deposits, including the Frasnian–Famennian marine biocrisis (McGhee, 1982). However, research on foraminifera of the Appalachian Basin has been very limited (Schieber, 2009). Further, investigations of North American Paleozoic foraminifera have been few, are dated, and almost exclusively limited to the Ohio and Illinois Basins, areas of the Midwest such as Oklahoma and Iowa, and some Rocky Mountain forelands (Moreman, 1930; Ireland, 1939; Stewart & Lampe, 1947; Summerson, 1958; Gutschick & Treckman, 1959; Gutschick et al., 1962; Conkin, 1961; Conkin & Conkin, 1964, 1982; Conkin et al., 1965; 1968).

Micropaleontology and biostratigraphy are integral for determining the stratigraphic record produced by paleoecological changes (e.g., global sea level changes, variable influences of tectonics, and climate). In the modern setting, both agglutinated and calcareous foraminifera are often abundant in deep and marginal marine depositional systems and prior research of modern marine systems has shown that certain foraminiferal assemblages can be directly correlated to certain environments and sea-level reconstructions worldwide (Scott & Medioli, 1980; Poag, 1981; Scott & Leckie, 1990; Goldstein et al., 1995; Ozarko et al., 1997; Saffert & Thomas, 1998; Patterson et al., 1999; Hippensteel et al., 2000; Lloyd, 2000; Leckie & Olson, 2003). Modern foraminiferal associations, or predominance facies (Poag, 1981; Culver, 1988), are consistent for certain genera in deep time well through the Mesozoic and into the Carboniferous (Tibert & Scott, 1999; Leckie & Olson, 2003; Velić, 2007; Dill et al., 2010; Bassi & Nebelsick, 2010; Gale & Kelemen, 2017). Through this investigation we seek to: 1) compile a first report on the foraminifera of the Late Devonian Appalachian Basin (Frasnian) in the gray and black shale sequences of western New York, and 2) determine if the use of well-established foraminiferal predominance facies can be successfully applied to known marine environments older than the Carboniferous.

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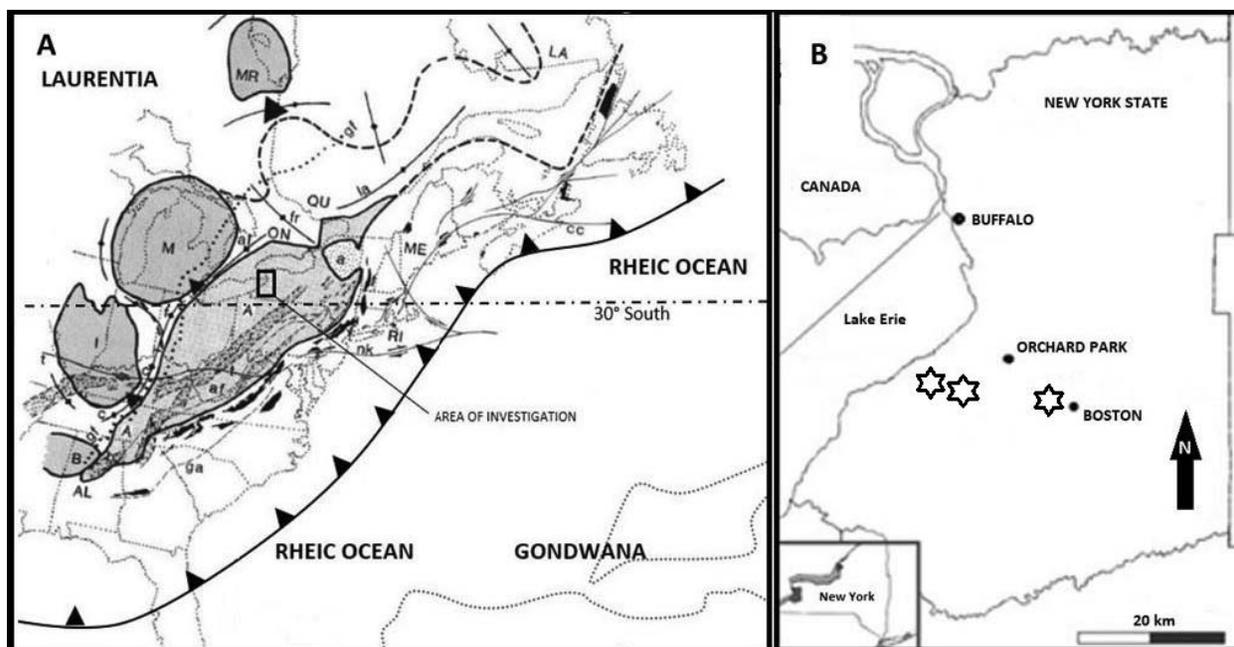
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FIGURE 1.   A) Paleogeographic reconstruction of Laurentia and the area of investigation, noted with a star, based on Ettensohn (2008) and Cocks &Torsvik (2011). Appalachian foreland basin and nearby structural features in eastern United States and southeastern Canada; dotted lines represent modern political boundaries. Preserved parts of the Appalachian foreland basin are shown in coarse stipple, and other possible parts of the basin to the northeast and northwest are outlined in dark dashes. The Black Warrior Basin (B) and the Illinois (I), Michigan (M), and Moose River (MR) intracratonic basins are shown in light stipple; cratonic arches (la, Laurentian arch; fr, Frontenac arch; al, Algonquin arch; f, Findlay arch; c, Cincinnati arch; r, Rome trough; k, Knoxville graben; b, Birmingham graben). Blackened areas east of the Appalachian Basin represent a chain of Grenvillian, Mesoproterozoic basement inliers or massifs, parts of the old continental margin transported westward during various Appalachian orogenies; the Adirondack massif (a). Other major structural features: the Grenville Front (gf), southern gravity anomaly (ga), the Allegheny Front (af), the 38th Parallel Lineament (t), the Ontario Embayment (o), the Quebec Basin (q), the Narragansett Basin (n), and a series of Carboniferous-Mesozoic strike slip faults (nk, N40-Kelvin fault zone; cc, Cobequid-Chedabucto fault zone). ME, Maine; Qu, Quebec; ON, Ontario; RI, Rhode Island; cpo, Coastal Plain overlap; and AL, Alabama. B) Map of Erie County, New York. Localities of sample collection denoted by stars.

GEOLOGIC HISTORY

The Paleozoic Appalachian Basin is one area of well preserved, relatively undeformed and unmetamorphosed sedimentary strata derived from erosion of the Acadian orogeny. The basin spans from Alabama northeasterly to Maine (Bradley et al., 2000) and was part of a retroarc foreland that developed adjacent and parallel to the Acadian Orogenic belt, a mountain chain built by oblique collision of the North American continental margin with the Avalon terrane beginning its formation at the Silurian-Devonian boundary (Bradley et al., 2000; van Staal et al., 2007, 2009; Ver Straeten, 2010; Fig. 1a). The Middle Devonian collision is referred to as the Neoacadian orogeny (van Staal et al., 2007). To the west lay the Laurentian epicontinental sea periodically breached, most likely not emergent at the interval of this investigation, by the Findlay-Algonquin Arch or a precursor arch (Cocks & Torsvik, 2011; Bingham-Koslowski, 2015). The dominant controls on the deposition of black shales in Devonian Appalachian Basin have been often been attributed to either or both global eustatic changes or tectonic events (Johnson et al., 1985; Ver Straeten et al., 1994; Brett et al., 1996; 2011; Werne et al., 2002; Sageman et al., 2003; Arthur & Sageman, 2005; Kohl et al., 2014). At the time of deposition, the beds studied herein were formed during a time of decreasing orogenesis (Ettensohn 1985a, b; Arthur & Sageman, 2005).

The Devonian mudrocks of western and central New York are part of the Catskill Delta Complex, dominated by siliciclastic material eroded from the Acadian orogen (Arthur & Sageman, 2005; Ver Straeten, 2010; Ver Straeten et al., 2011). Water depths within the basin are highly debated (see Smith et al., 2019; Ver Straeten et al., 2019). However, recent paleobathymetric works based on distributions of lithofacies, conodont biofacies, and stratigraphic architecture show that water depths in the distal part of the Appalachian Basin are characterized by shelf to upper slope depths ($\leq$300 m at maximum highstands); the craton-ward side of the basin is suspected to average about 70–75 m (Ettensohn, 1985a, b; Vogel et al., 1987; Schieber, 1994; Sageman et al., 2003; Arthur & Sageman, 2005; Brett et al., 2011; Ver Straeten et al., 2011; He et al., 2019).

The Upper Devonian beds of western New York have been studied in depth and the subsequent reports on the lithology, stratigraphy, and geochemistry of the beds that recorded a series of 3rd order depositional sequences (Becker et al., 2012), hundreds of thousands to a few million years each in their duration. Further, coeval marine biotic crises have been well documented displaying alternating beds of deeper water, dark gray organic-rich shale, suspected to be deposited due to shifting oxygen conditions within the water column and bottom waters (Sageman et al., 2003; Arthur & Sageman, 2005; Boyer & Droser, 2011; Boyer et al., 2011; Ver Straeten et al., 2011; Haddad et al., 2018; Kelly et al., 2019;

He et al., 2019; see Smith et al., 2019 and comments by Ver Straeten et al., 2019), and light gray organic-poor shale deposited in shallower, more oxygenated water (Ver Straeten et al., 2011). The shale units investigated here are just a few of many gray to black shale sequences spanning the Middle to Late Devonian and considered distal basin marine beds of the deltaic wedge during decreasing orogenesis and a long-term eustatic transgressive succession (Johnson et al., 1985). The Cashaqua Formation (uppermost unit of the Sonyea Group), the Rhinestreet and Angola formations (West Falls Group), and the Pipe Creek and Hanover Shale formations (Java Group) accumulated in the relatively enclosed northern part of the northeast-southwest trending Appalachian foreland basin, which is bounded on its east and southeast by the rising Acadian Highlands (Arthur & Sageman, 2005; Ver Straeten, 2010; Ver Straeten et al., 2011), spanning the middle to uppermost Frasnian.

The Cashaqua Formation is a gray shale with an abundance of often flattened ellipsoidal limestone nodules and a few thin layers of black shale. The Cashaqua grades eastward into a thickening sequence of siltstone and silty shale and is part of a common turbidite facies of the Catskill Delta (Wilson & Schieber, 2015) with a total organic carbon (TOC) that varies from 0.46% at the bottom of this interval to 1.3% at its top where it is sharply overlain by the organic-rich Rhinestreet Formation (Sageman et al., 2003). Lash (2019) noted that the uppermost ~40 cm of the Cashaqua through the lowermost Rhinestreet represents the termination of a muted North American expression of the *punctata* event. The Sonyea Group is overlain by the West Falls Group (Rhinestreet and Angola Shale formations), which is in turn overlain by the Java Group (Pipe Creek and Hanover Shale formations).

The Rhinestreet Formation, the basal shale unit of the West Falls Group, is a thick, fissile, black shale that thickens rapidly from west to east and interfingers and grades with the overlying gray Angola Shale Formation (Wilson & Schieber, 2015). The percent TOC (wt%) of the Rhinestreet shale, a heavily fractured black and gray shale, at its base along the Eighteenmile Creek section is 8.09wt% and diminishes upward in the column to 2.3wt% at the Angola shale contact (Sageman et al., 2003).

At the base of the overlying Java Group, marking the onset of the Kellwasser event (Over, 1997, Bush et al., 2015), is the thin, black Pipe Creek Shale Formation (1 m thick bed in western New York). The Pipe Creek is a persistent, organic-rich black shale throughout its lateral extent (Wilson & Schieber, 2015). The Hanover Shale is a gray shale, with some interbedded black shale beds. Like the aforementioned shale beds, the Hanover also thickens to the east grading into silty shale, siltstone, and sandstone (Wilson & Schieber, 2015). The TOC content rises from <1 wt% in the Angola to an average of 4 wt% in the Pipe Creek, and then falls back to <1 wt% in the Hanover (Sageman et al., 2003).

METHODS AND MATERIALS

Shale samples were collected through the middle to upper Frasnian Cashaqua, Rhinestreet, Angola, Pipe Creek, and Hanover formations from three localities in western New York. Sampling of materials began at 1 m below the Cashaqua-Rhinestreet contact along Eighteenmile Creek in Eden, New York (42°41′56.00″N, 78°56′20.36″W; Fig. 1b). Samples were taken at 75 cm below the contact and from 40 cm below the contact the shale was sampled at 10-cm intervals until half a meter above the contact. The justification for this level of detail is that this interval includes the reference section for a damped North American expression of the *punctata* event, an extreme ^{13}C excursion within the *Palmatolepis punctata* conodont zone prior to rapid eustatic shifts recorded at this point in the stratigraphic record. After the half-meter point above the contact, samples were taken at 25-cm intervals up to 1 m above the contact; above this level samples were taken at 2- or 3-m intervals, depending on outcrop accessibility, up to the Rhinestreet-Angola transition (Scraggy Beds; Luther, 1903) zone (12 m total). The uppermost Rhinestreet and lower Angola formation samples were taken from an outcrop under the railroad track overpass just off of Belknap Road, Eden, New York (42°41′15.64″N, 78°52′39.01″W).

Samples collected from the uppermost Angola and lower Hanover shales were taken at 0.5 and 1m intervals above and below the Pipe Creek Shale, 4 samples throughout this 1 m exposure were selected at random, based upon outcrop exposure and accessibility along Route 219 and the Zimmerman Avenue overpass outside of Boston, New York (42°39′08.91″N, 78°45′58.74″W; Pipe Creek, Angola, and 0–4 m Hanover; Fig. 1b).

The shale samples were prepared following the methodology of Meehan et al. (2020); coarsely crushed with a mortar and pestle, completely submerged in an undiluted industrial grade quaternary surfactant (Betco Quat Stat 5), bottled, capped, and set in a sonic bath until the shale was completely dissolved. Aliquots were run through a series of nested sieves (355, 212, 90, and 63 μm).

RESULTS

The lithology of black, dark gray, and gray shale sediments correlates to previously published research on the beds. All shale formations, black to light gray in color, are reflective of the interpreted basinal settings of the Catskill Delta complex (Table 1).

Fifty-five species (N) from 27 genera were identified. Foraminiferal assemblages for all shale formations are dominated by agglutinated species (75%) predominantly from the order Astrorhizina (49% of total population; Table 1; Figs. 3–4). While calcareous species are present in all formations, there is a notable increase in their diversity (species of Miliolida; Table 1) and occurrence within the Angola and Hanover formations; calcareous species occur more frequently and in higher abundance within light gray Angola and Hanover Shale members. Calcareous genera *Tolypammina* and *Trepeilopsis* had the lowest frequency of occurrence and species diversity in the black Rhinestreet Shale but increased in abundance within the Angola and Hanover shales. Species of *Reophax* and *Saccammina* were found in nearly all shale samples; other dominant genera in all shale members include *Lagenammina* within the Cashaqua through lower Rhinestreet, *Oxinoxis* within the upper Rhinestreet through the Upper Angola, and *Ammobaculites* within the Angola and Hanover (Table 1).

TABLE 1. Foraminiferal numbers of the genera of foraminifera found from samples within the upper Sonyea, West Falls, and Java Formations of the Devonian Appalachian Basin.

	Cashaqua					Rhinestreet															Angola				PC	Hanvover							
height (m)	-0.75	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2	0.3	0.4	0.5	0.6	0.75	1	2	3	6	10	11	12	-4	-3	-2	-1	0	0.5	1	3	4	5	6	7	8
Ammodiscidae	2.3	3.1	2.9	4.2	3.6	7.1	3.2				4.8			3.1		4.3	7.1	5.3	6.3	6.3			2.3	2.8	2.6					10.0	3.4		9.5
Ammovertella					3.6																				2.6						3.4		
Bathysiphon		3.1	5.9		3.6	14.3	12.9		3.8							4.3					1.2		2.3	2.8	4.5	5.3							
Blastammina			5.9				3.2	3.4												6.3	1.3									5.3			
Colomammina																					1.3				2.3								
Hemisphaerammina																									2.3								
Hyperammina	8.7		2.3	4.2		7.1	2.1	6.3	11.5	4.2	8.7			18.2	10.0	13.0		21.1	6.5	6.3			5.9	2.8	6.3			5.3			6.9		4.8
Lagenammina	37.6	39.2	24.3	27.7	17.8	21.2	18.5	14.5	7.7		19.0	16.7			10.0	17.4	21.4	5.3	6.5	6.3	4.7	7.7	3.2	2.8	6.3	5.3		5.3			6.9	11.1	
Orinosis	8.7				3.6	7.4			3.8		8.6			27.3	10.0	3.0	21.4	5.3	3.1	12.5	2.3	2.6	8.8	5.5	2.3		5.3	5.3	5.3	4.1		5.6	9.5
Proteonina		3.1			10.7	7.4												10.5		6.3	2.3	2.6	3.2	8.3	11.4	2.6		1.3			17.2	5.6	9.5
Psammosphaera			2.3			7.1	2.1	3.4													3.1		1.7	2.8	6.8	2.6		1.3		15.0		5.6	
Reophax		4.2	2.3	8.3	10.1	7.1	13.0	13.8	11.5	12.3	14.3	16.7	14.3		10.0		7.1	10.5	6.3	12.5	10.4	8.1	8.8	8.3	4.5	10.5	10.5	13.2	5.3		6.3		9.5
Saccammina	19.7	28.1	11.7	15.6	11.4	14.8	12.5	27.6	19.4	24.7	31.1	50.0	28.6	18.2	30.0	8.7	7.1	16.0	27.6	12.5	13.9	12.5	8.9	11.1	17.9		9.2	10.5	17.6	15.0	13.8	11.1	4.8
Sorosphaera		4.2	8.8	8.3	14.3						6.3										5.1		1.7	2.8		2.6		6.1	5.3	8.2	3.4		
Tholosina			2.3	4.2				3.2	3.4	11.5	4.6					10.0						2.6		2.8	6.8		5.3	1.3				5.6	
Thurammina	3.1		5.9	8.3	3.6	16.1					4.1						7.1	5.3		6.3		1.5	1.7		4.5				5.9	4.1			
Thuramminoides	5.3	7.4	8.8	4.2	7.1		5.3	3.4	11.5	12.5		16.7			4.2				18.8	6.3	3.1			5.5		2.6		4.6			3.4	5.6	
Tolypammina			8.8	11.0	7.1	7.1	5.3	13.8	11.5	20.8	4.8		28.6	27.3	10.0	21.7	7.1	5.3	12.5	6.3	15.1	17.9	16.2	13.9	4.5	15.0		4.6	5.3	15.0	17.2	11.1	13.0
Trochammina		5.6	2.3		1.2						8.3											5.2		2.8		2.6			5.9	8.2	3.4	5.6	9.5
Webbinelloides	3.0	5.6	2.3	4.2	1.2					4.2	4.8					10.0	8.7	14.3	5.3	6.3	5.6	5.1	1.7	2.8	4.5	5.3	5.3		5.9	4.1		5.6	
Pseudastrorhiza					1.2				3.4												3.1				2.3		5.3	4.6		4.1			
Raibosammina (?)										7.7			14.3							6.3													
Sorosphaeroidea									3.4												1.2	1.5	6.3	8.3		10.5	7.1	6.1	17.6				4.8
Ammobaculites								3.2	6.9		8.3			14.3							25.7	22.4	21.7	8.3	9.1	14.2	15.5	21.5	11.8	4.1	10.2	11.1	9.8
Psammophax																						5.1	2.9	2.8		2.6	5.3						
Schizammina																4.2					1.2	2.6	1.7				5.3		5.3		3.4	11.1	4.8
Stegnammina																								2.3									
Trapdopsis																						1.5		2.8	2.3	10.5	15.8	4.6		8.2		5.6	4.8
Webbinella																	4.2	7.1	10.5			1.5			2.3	2.6	10.5	4.6					
(N_species)	11	11	18	18	22	11	17	18	17	15	9	5	7	10	9	12	10	15	11	15	22	20	22	25	26	23	17	23	13	14	14	16	17
total	100.4	100.4	100.7	100.1	100.0	100.8	100.7	111.0	100.2	99.9	100.1	100.0	100.0	100.0	100.0	100.0	100.0	100.2	100.0	100.0	100.6	100.4	100.3	100.0	100.5	100.3	100.2	100.1	100.0	100.1	99.9	100.0	100.3

Two genera occur exclusively within gray shales (*Ammovertella*, *Psammophax*) and two genera were nearly exclusive to gray shales, with the exception of single specimens found ≤20 cm from the Cashaqua-Rhinestreet contact (*Sorosphaera* and *Sorosphaeroidea*). Two genera were found exclusively in black shales (*Hemisphaerammina* and *Stegnammina*).

The Rhinestreet Shale had the lowest diversity and occurrence of species (55 species from 27 genera; Table 1); there is a notable rapid drop in $N_{species}$ before the dense black shale sample at ~60 cm above the Cashaqua-Rhinestreet contact, ~3.5 m above the peak of the ^{13}C excursion of the *punctata* event (Lash, 2019). This drop in $N_{species}$ is followed by a very slow recovery that begins to stabilize in the upper 3 m of the Rhinestreet Shale until in the Scraggy Bed where the Rhinestreet then begins to transition into the Angola Shale (Table 1). The number of species found within the Angola Shale is slightly more robust ($N_{species} = 20$–22) in comparison to the uppermost Cashaqua ($N_{species} = 11$–22) prior to the onset of the *punctata* event. The meter-thick bed of the Pipe Creek had the highest $N_{species}$ (26), several of which occur exclusively in Pipe Creek (Table 1). There is a notable shift in generic dominance from *Lagenammina* in the Cashaqua and lower Rhinestreet (Table 1) to *Saccammina* in the mid- to upper-most Rhinestreet and Pipe Creek (Table 1) and finally to an *Ammobaculites*-dominated assemblage in the Angola and Hanover shales (Table 1).

Overall, the majority of species in all beds are semi-infaunal or infaunal dwellers (74%) with 21% epifaunal dwellers; the remaining 5% are variable in habitat from epifaunal to infaunal dwellers (Table 2). The highest occurrence of epifaunal dwellers is found in the Angola Shale

and Hanover Shale members. The genera found in samples throughout the upper Sonyea Group and the West Fall Group are consistent with Poag's (1981) modern inner neritic predominance *Saccammina-Ammobaculites* facies and Culver's (1988) foraminiferal depth zonation for a deltaic system with depths of 0–50 m. The consistency of observed genera suggests relatively similar potential depths; however, there is a distinct shift in the ratio of agglutinated to calcareous genera found in the shale formations. Ratios of agglutinated to calcareous specimen counts are consistent from the upper Cashaqua through the Rhinestreet with agglutinated genera averaging ~80% of all samples collected for these units (4:1; Table 2; Fig. 2). Within the Angola Shale, this ratio flips to calcareous-dominated specimen counts (40% agglutinated to 60% calcareous or 2:3; Table 2; Fig. 2) in the lower 3–4 m. In the upper 1–2 m section of the Angola Shale this ratio reverses to 60% agglutinated to 40% calcareous (3:2; Table 2; Fig. 2). The ratios of Pipe Creek samples revert to values similar to those of the Rhinestreet and Cashaqua with approximately 80% agglutinated (4:1; Table 2; Fig. 2). The samples from the lower meter of the Hanover are dominated by calcareous specimens most like that of the samples from the 3–4 m levels of the Angola Shale (2:3; Table 2; Fig. 2). The remainder of the Hanover samples are only slightly dominated by agglutinated genera, in the 1–2 m samples of the Angola (3:2; Table 2; Fig. 2). There is a distinct peak in the total organic carbon (TOC) found within Pipe Creek, particularly compared to that of the adjacent shales (Angola and Hanover). When the foraminifera type is cross-plotted with TOC, there is no distinct relationship found between foraminiferal type and TOC.

TABLE 2.   Morphological based assignments of life mode and feeding strategies as assigned by Koutsoukos & Hart, 1990; Flach et al., 1998; Reolid et al., 2008a, b.

MORPHOGROUP	TEST TYPE	LIFE MODE	FEEDING STRATEGY
TABULAR - cylindrical			
Hyperammina	agglutinated	infaunal	detritivore
Bathysiphon	agglutinated	infaunal	detritivore
Reophax	agglutinated	infaunal	detritivore
Rockfordinia	agglutinated	infaunal	detritivore
Stegnammina	agglutinated	infaunal	detritivore
GLOBULAR			
Thuramminoides	agglutinated	shallow-infaunal	detritivore
Thurammina	agglutinated	shallow-infaunal	detritivore
Oxinoxis	agglutinated	infaunal	detritivore
Psammosphaera	agglutinated	infaunal	detritivore
Webbinelloides	calcareous	shallow-infaunal	omnivore
Webbinelloidea	calcareous	shallow-infaunal	omnivore
Blastammina	agglutinated	infaunal	detritivore
Hemisphaerammina	agglutinated	infaunal	detritivore
Psammosphax	agglutinated	infaunal	detritivore
PLANOCONVEX			
Sorosphaera	agglutinated	infaunal	detritivore
Trochammina	agglutinated	shallow-infaunal	omnivore
Colonammina	agglutinated	infaunal	detritivore
Webbinella	agglutinated	shallow-infaunal	omnivore
Sorospheara	agglutinated	infaunal	detritivore
Blastammina	agglutinated	infaunal	detritivore
Tholosina	agglutinated	infaunal	detritivore
ELONGATE			
uniserial, initial coiled phase			
Ammobaculites	calcareous	epifaunal	detritivore
subcylindrical tapered			
Lagenammina	agglutinated	infaunal	detritivore
Proteonina	agglutinated	infaunal	detritivore
Tolypammina	calcareous	epifaunal	herbivore
Ammovertella	agglutinated	infaunal	detritivore
FLATTENED			
unilocular			
Ammodiscadae	agglutinated	epifaunal	detritivore
Saccammina	agglutinated	infaunal	detritivore
irregular			
Riabosammina	agglutinated	infaunal	detritivore
IRREGULAR			
Trepeilopsis	agglutinated	epifaunal	omnivore

DISCUSSION

PREDOMINANCE FACIES & BENTHIC FORAMINIFERAL DEPTH ZONATION

Micropaleontology has played major roles in deciphering the stratigraphic record. It is well established through the original works of Poag (1981) and Culver (1988) on neritic communities of Cenozoic foraminifera that marine environments and bathymetry can be determined through the dominance of certain genera. Shifts in neritic benthic foraminiferal assemblages occur as a result of changes in relative sea level due to variables such as tectonics, glacio-eustasy, and climate; these have been well documented in modern, Cenozoic, Mesozoic and the late Paleozoic strata (e.g., Poag, 1981; Culver & Buzas, 1981; McGowran & Li, 1996; Li & McGowran, 1997; Tilbert & Scott, 1999; Huber et al., 2004; Hearty et al., 2007; Nugraha et al., 2019). Simply, they act as a coherent unit over geologic time; genera assemblages do not change composition through the sequences.

Distributions of benthic foraminifera along modern terrigenous margins have demonstrated the usefulness of distinguishing biofacies on the basis of predominant genera within research investigations for over 40 years. Environmental changes, often but not exclusively, associated with fluctuating sea level are known to result in changes in community structure and extinctions (Koutsoukos & Hart, 1990; Kennett & Stott, 1991; Kaiho, 1992, 1994, 1999; Speijer et al., 1996; Speijer & Van der Zwaan, 1994; Culver & Buzas, 2000; Alegret et al., 2001; Holbourn & Kuhnt, 2001; Holbourn et al., 2001; Leckie & Olson, 2003; Davydov et al., 2014, 2016). Prior investigations of the Upper Devonian shale beds in western New York have shown repeated shifts in relative sea level.

The foraminiferal assemblages of shale members of this investigation are dominated by three main genera: *Lagenammina*, *Saccammina*, and *Ammobaculites*. *Saccammina* and *Ammobaculites* are associated with shallow water (0–50 m; Poag, 1981) and inner neritic settings (0–50 m; Culver, 1988). While *Lagenammina* is not incorporated into the works of
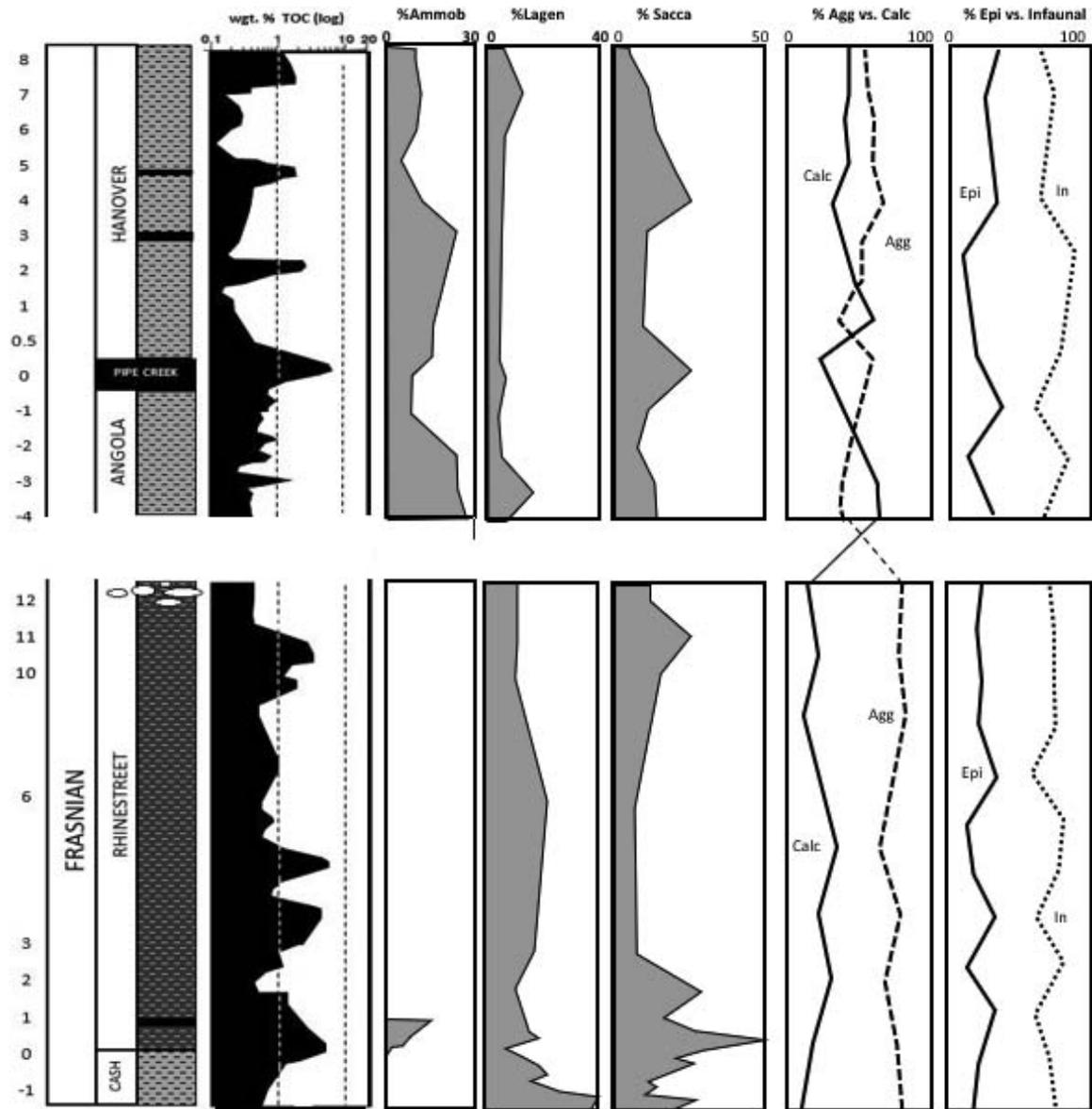
FIGURE 2. Stratigraphic sections studied select dominant species of *Saccammina*, *Lagenammina*, and *Ammobaculites* and their percent of total population samples throughout the section, percentage of agglutinated to calcaerous species and percentage of epifaunal to shallow and deep infaunal species found. Sampling in the lowermost Rhinestreet and uppermost Cashaqua (2 m) done at a 10-cm scale.

Poag and Culver, it is considered by micropaleontologists to be a sister taxon of *Saccammina* and most commonly reported in paleoenvironments spanning shallow subtidal and reef settings, although such settings have never been identified in this area west of the deltaic complex (Loeblich & Tappan, 2015). Thus, we suspect the presence of known opportunistic foraminiferal species like *Lagenammina* and *Saccammina* in these shale units is most likely a reflection of depth. Although confirming *Lagenammina* as a biofacies indicator like *Ammobaculites* and *Saccammina* is beyond the scope of this work, we suspect that this genus, and potentially others herein, may be reflective of more nuanced changes in paleoecological conditions and depths in this portion of the deltaic com-

plex; this warrants further investigation on a much larger scale.

BENTHIC FORAMINIFERA AS PALEOECOLOGICAL INDICATORS

Benthic foraminiferal taxa are important indicators of physicochemical parameters at the seafloor and indirectly reflect environmental signals of the water column (Jorissen et al., 1995; 2007). Studies of both modern and ancient foraminiferal assemblages have shown that shell morphology, coiling mode, the existence of pores, and aperture type are reflective of different lifestyles and feeding strategies and serve as useful proxies for identifying marine environments such as lagoons, marshes, and deltaic systems
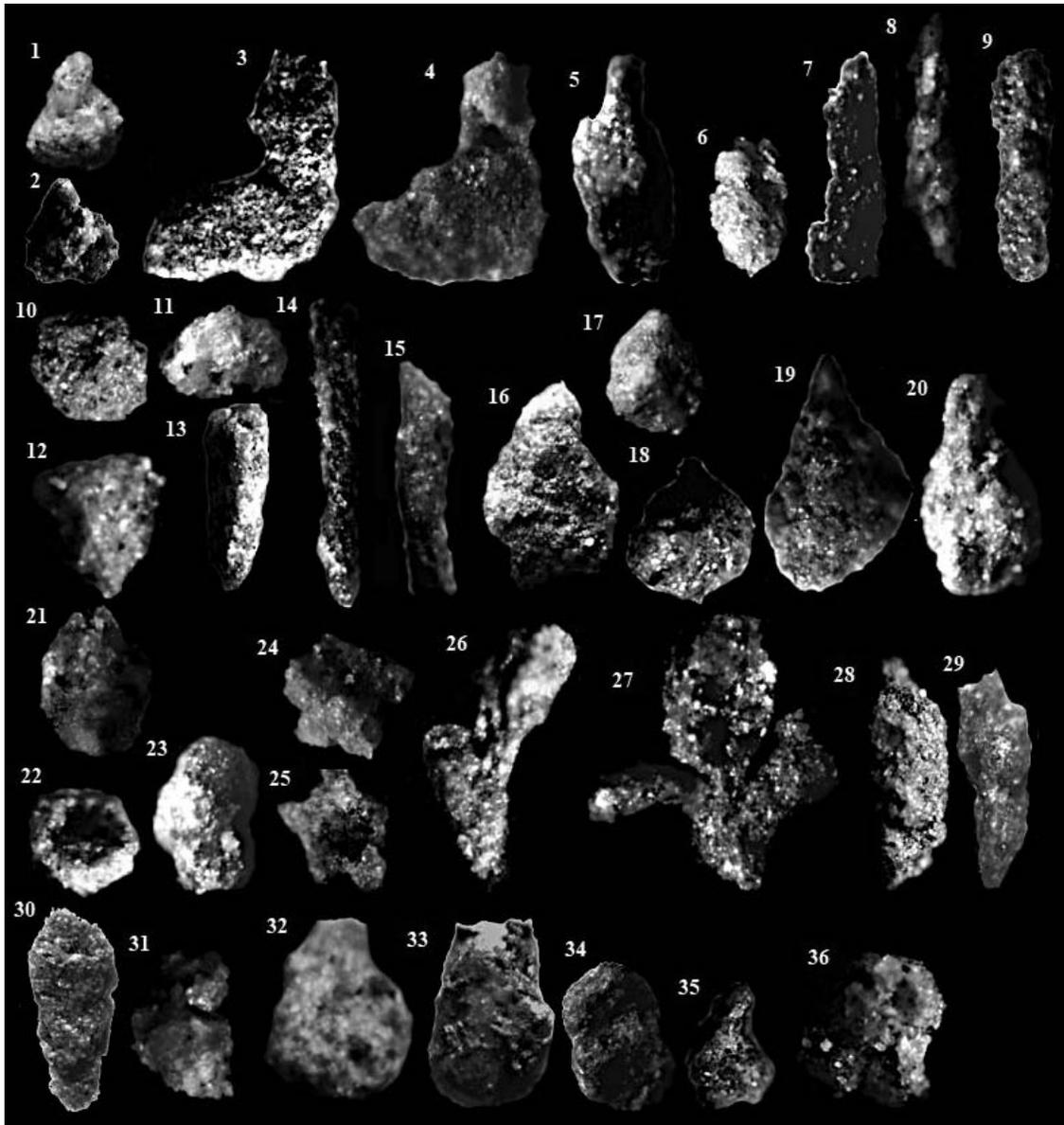
FIGURE 3. **1** *Ammobaculites pyriformis* Gutschick and Treckman. **2** *Ammobaculites beveridgei* Conkin and Conkin. **3** *Ammobaculites minutus* Waters. **4** *Ammodiscidae* sen. et sp. indet. **5** *Ammodiscus longexsertus* Gutschick and Treckman. **6** *Ammovertella* sp. **7** *Bathysiphon diminutionis* Moreman. **8** *Bathysiphon rugosus* Ireland. **9** *Bathysiphon* sp. **10** *Blastammina eisenacki* Conkin, Conkin and Young. **11** *Colonammina verruca* Moreman. **12** *Hyperammina casteri* Conkin. **13** *Hyperammina constricta* Gutschick and Treckman. **14** *Hyperammina rockfordensis* Gutschick and Treckman. **15** *Hyperammina* sp. **16** Lagenammina stilla Dunn. **17–18** *Oxinoxis ligula* Gutschick, Weiner and Young emend. Conkin and Conkin. **19** *Proteonina cumberlandiae* Conkin. **20** *Proteonina* sp. **21** *Proteonina wallingfordensis* Conkin. **22** *Psammosphae* sp. **23** *Psammosphax hormiscoides* Summerson. **24–25** *Psuedoastrorhiza concica* Gutschick, Weiner and Young. **26** *Raibosammina* sp. (?). **27** *Schizamminna* sp. **28** *Rockfordinia lachrymose* Gutschick and Treckman. **29** *Reophax northviewensis* Conkin and Conkin (1964). **30** *Reophax* sp. **31** *Psammosphax bipartita* Ireland. **32** *Saccammina pseudospiralis* Cushman and Stainbrook. **33** *Saccammina* sp. **34** *Sorosphaera bicelloidea* Stewart and Lampe. **35** *Sorosphaera columbiense* Stewart and Lampe. **36** *Sorosphaera trichora* Summerson.

(e.g., Corliss, 1985, 1991; Jones & Charnock, 1985; Bernhard, 1986; Tyszka, 1994; Nagy, 2009; Smoleń, 2012). The use of morphological categories in paleoecological studies, instead of species-level taxonomic assignment, is advantageous in that morphology allows for reliable comparisons of assemblages of different age, reducing the effect of evolutionary divergence of habitat within lineages. Nagy (1992, and numerous subsequent publications) has shown that de-

termining taxonomy at the species level is not required for determining the life guilds and niches (Tyszka, 1994; Reolid, 2008a, b; Nagy et al., 2009; Smoleń, 2012; Colpaert et al., 2017). Several distinct species within identified genera were found. However, the published literature on Devonian foraminifera in this area of the Appalachian Basin are limited and should be revisited by specialists in this field. Thus, we did not pursue identification and analysis at the
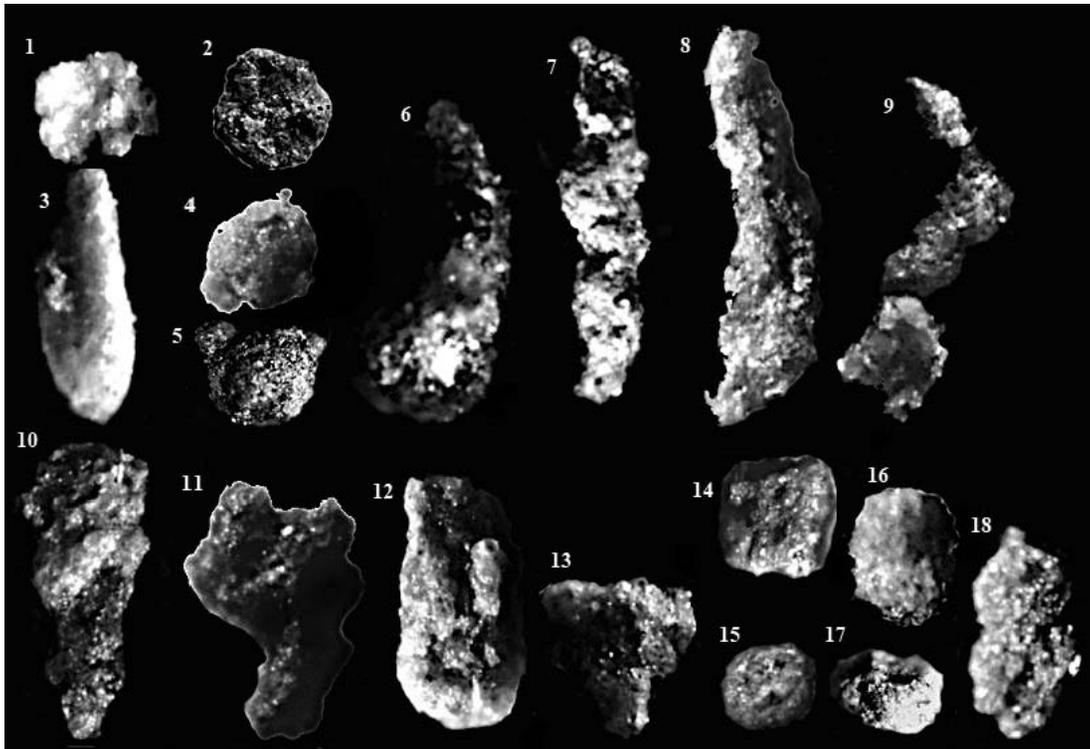
FIGURE 4. **1** *Sorosphaeroidea pentachora* Summerson. **2** *Tholosina* sp. **3** *Thuramminoides sphaeroidalis* Plummer emend. Conkin. **4** *Thurammina tubulata* Moreman. **5** *Thurammina arcuata* Moreman. **6** *Tolypammina bulbosa* Gutschick and Treckman emend. Conkin and Conkin. **7** *Tolypammina jacobschapelensis* Conkin. **8** *Tolypammina* sp. **9** *Tolypammina sperma* Gutschick, Weiner and Young. **10** *Trepeilopsis glomospiroides* Gutschick and Treckman. **11** *Trepeilopsis reczurvidens* Gutschick and Treckman. **12** *Trepeilopsis spiralis* Gutschick and Treckman. **13** *Trepidiopsis* sp. **14** *Trochammina mehli* Conkin and Conkin. **15** *Webbinelloidea hemispherica* Stewart and Lampe. **16** *Webbinelloides nodosa* Summerson. **17** *Webbinella bipartita* Ireland. **18** *Webbinelloides similis* Stewart and Lampe.

species level in order to avoid rendering a biased population-based analysis. We found that limiting our identification of specimens to the genus level still yields useful and insightful results.

Benthic foraminiferal morphologies have been described and assigned to morphogroups that reflect lifestyles and feeding strategies (Jones & Charnock, 1985; Bernhard, 1986; Corliss & Fois, 1990; Corliss, 1991; Nagy, 1992, 1995; Tyszka, 1994; Szydło, 2004, 2005; Reolid et al., 2008b). The use of morphology to determine these factors is not without limitations. Buzas et al. (1993) found that the use of morphology to determine lifestyle (preferred depth) led to correct interpretations about 75% of the time. They further determined, and subsequent publications have verified, that many species with a known preferred depth zonation are capable of mobility and would move up within the sediment to take advantage of more hospitable conditions; deep infaunal species can easily inhabit shallow infaunal to epifaunal depths. Buzas et al. (1993) further suggested that the term epifaunal be restricted in its application to hard substrates or more coarsely textured sediments (e.g., sand) as many species found with their investigation were living within the sediment rather than being restricted to the sediment-water interface.

The depth in the sediment at which benthic foraminifera live is predominantly determined by oxygen and nutrient availability (Tyszka, 1994; Jorissen, 1995; Van der Zwaan et al., 1999; Ernst & Van der Zwaan, 2004). Oxygen levels and available nutrients are determined by two main sources: autochthonous sources, driven primarily through photosynthetic production within the environment, and allochthonous sources which derive from other incoming waters, usually in relation to detrital influx (Hupp et al., 2019). An epifaunal life mode is advantageous in environments with nutrient and/or oxygen limitations; however, in environments with high organic content, such as deltaic assemblages, the sediment is often dominated by foraminifera with an infaunal life mode. Further, opportunistic behavior of some taxa is often related to nutrient input where an increase in nutrients, autochthonous or allochthonous, is favored by opportunistic foraminifera and reflected in their increasing population numbers; this produced a reduction in the foraminiferal diversity signal (Sjoerdsma & Van der Zwaan, 1992). However, in situ observations of modern benthic taxa have shown that some genera are adaptable to changes in food availability and changing environmental conditions (e.g., Buzas et al., 1993; Linke & Lutze, 1993). The flexibility in behavior is considered a dynamic adaptation to optimize food acquisition, rather than a static concept leading to habitat classification, and so we use this concept of morphogroup assignment (in terms of both feeding strategy and life mode) with caution rather than as an absolute, particularly for extinct genera without a well-studied ancestor.

Overall, nearly 76% of the genera and total specimens collected were interpreted as detritivores (detritus suspension feeders or deposit feeders); herbivores constitute 7% of the assemblages and omnivores constitute 17% of the assemblages (as assigned by Koutsoukos & Hart, 1990; Flach et al., 1998; Reolid et al., 2008a, b). The shifts in relative abundance of feeding strategies reflect similar trends found from life modes in that the populations shift from a dominance of omnivorous foraminifera (≤40%) within gray shales to almost entirely detritivores within black shales (≤75%). The shifts within feeding strategy agree with previously published research on changes in primary productivity, deepening, hyperpycnal events, and potential dysaerobic, anaerobic, and eutrophic conditions (Arthur & Sageman, 2005; Lash, 2016, Haddad et al., 2018; Kelly et al., 2019). Further, the feeding guild composition of the foraminiferal assemblages is consistent with modern deltaic foraminiferal assemblages known to take advantage of allochthonous detrital food sources (Nagy et al., 1995). Thus, all three foraminiferal assemblages (based on life mode and feeding strategy) are reflective of populations found in modern deltaic systems and correlate to well documented shifts noted in the lithology, conodont biofacies, magnetic susceptibility, and geochemistry of these members.

Benthic foraminiferal faunas usually inhabit a depth of several cm of the superficial sediment layer. This by nature coincides with a range of well oxygenated to strongly hypoxic conditions. Faunas typical of environments with well-oxygenated bottom waters often contain a mixture of taxa that inhabit fully oxic to strongly hypoxic or even anoxic microhabitats. While individual species are known to have a preference for a specific depth interval, even taxa considered to be epifaunal do not live exclusively at the sediment-water interface, have the ability to migrate through the uppermost millimeters to centimeters of the sediment and survive within a wide range of oxygen concentrations (e.g., Barmawidjaja et al., 1992; Ohga & Kitazato, 1997).

There is a complex interplay between export productivity and oxygenation of bottom and pore waters in benthic ecosystems. The competitive ability of most species to survive and thrive appears to be determined by one or both of these parameters. Jorissen et al. (1995) suggested that deep infaunal taxa, often considered indicative of hypoxic conditions, are only present when the organic flux is sufficiently high to have organic detritus within the sediment that can be used metabolically. In areas with lower flux rates most organic matter is consumed at the sediment-water interface, and deeper sediment layers are too poor in organic matter to be inhabited by deep infaunal taxa.

For the foraminiferal populations of the Devonian deltaic complex in western New York, the predominance of deep infaunal (flattened unilocular *Saccammina*-dominated assemblages), suggest episodes of either reduced oxygen availability or water column stratification in the black shale formations (high TOC Rhinestreet and Pipe Creek formations). The sudden appearance of deep infaunal taxa in the fossil record also may be the result of an increased organic flux and not of lowered bottom water oxygen concentrations as previously suggested. Herein, deep infaunal assemblages persist beyond black shales well into gray shale members. Deep infaunal taxa are dominant throughout the entirety

of samples in this investigation, as in many deltaic systems, suggesting that there was a continuous supply of organic detritus and oxygenation conditions within the uppermost sediments were at least hypoxic rather than anoxic (Jorissen, 1999; Murray, 2001).

Within the gray shale formations (Cashaqua, Angola, and Hanover), the relative percentage of epifaunal foraminifers rises indicating a general increase in oxygen availability. However, the uptick in epifaunal taxa within gray shale members is not persistent throughout those beds. Similar peaks, never exceeding 40% of all assemblages, also occur within black shale formations and could be reflective of freshwater inundation or pycnocline (Lash, 2016), seasonal shifts in paleoproductivity (Sageman et al., 2003), or nutrient starvation (Arthur & Sageman, 2005). Haddad et al. (2018) investigated drill cores spanning the Lower Kellwasser Event (Pipe Creek) in western New York by using trace metal proxies (e.g., Mo, Mn, U, and V), Fe mineral speciation, paleoproductivity proxies (Ba), ichnofossil assemblages, and lipid biomarkers. Their work provided evidence through lipid biomarkers that support prior interpretations of variable dissolved oxygen conditions (Murphy et al., 2000a, b; Werne et al., 2002; Sageman et al., 2003; Boyer & Droser, 2011; Boyer et al., 2011), pointing to seasonal and rare episodes of euxinia rather than persistent anoxic/euxinic conditions. Kelly et al. (2019) noted that the varying abundances of organic-walled microfossils in the Lower and Upper Kellwasser event beds of the Pipe Creek and upper Hanover shales, respectively, exhibited geochemical signals of dysoxic conditions potentially brought on by seasonal eutrophication. Detailed sampling within this investigation was limited to the uppermost meter of the Cashaqua and lowermost Rhinestreet. There is clear evidence of rapid shifts in certain species (*Lagenammina*, *Saccammina*, and *Ammobaculites*) within this interval (Fig. 2) that may be interpreted as episodes of short-lived relative sea-level rise events or shifting paleoecological conditions beyond water depth. Prior investigations have shown that this was a period of decreased orogenic uplift.

Traditionally, the black shale members were considered to have been deposited under anoxic conditions, however recent work has suggested the Rhinestreet may well be reflective of a combination of the aforementioned mechanisms (Arthur & Sageman, 2011; Ver Straeten et al., 2011; Lash, 2016). Based upon foraminiferal assemblages and their lack of differentiation between gray and black shale beds, these beds were most likely deposited in substantially shallower depths than traditionally accepted. On this basis and the work of Haddad et al. (2018), we feel that an expansion of microfossil investigations and further implementation of geochemical proxies will better constrain the paleoecological conditions surrounding the massive black shale formations and their associated marine crises.

Foraminiferal Assemblages & Late Devonian Marine Crises

The duration and causes of Devonian mass extinctions have been the focus of considerable debate and interpretation for decades. Some investigations have suggested that the Frasnian-Famennian event was a single prolonged marine

biotic crisis lasting 20–25 Ma that was punctuated by 7 to 10 smaller extinctions (Hallam & Wignall, 1997; Algeo et al., 2000; Hallam & Hallam, 2005; Kiessling & Simpson, 2011). Other researchers argue that there were two crises of prolonged biodiversity losses followed by two extinction events of much shorter duration (Schindler, 1990; McGhee, 1996; Walliser, 1996).

The Devonian Period contains evidence of a series of marine crises that are recorded globally, a few of which (in western New York in particular) correlate to the deposition of black and gray shale sequences or limestones, and accentuated pelagic faunal turnovers (e.g., House, 1996; Haddad et al., 2018; Kelly et al., 2019, Lash, 2019). The events which straddle the beds of this investigation are the *punctata* event (Rhinestreet event), the Lower Kellwasser Event (Frasnian, with the Lower Kellwasser Event at the Pipe Creek, ~372 Ma and second and more severe Upper Kellwasser Event in the uppermost Hanover Shale; Schindler, 1990; Buggisch, 1991; McGhee, 1996). The latter event impacted up to 80% of marine species (Hallam & Wignall, 1997).

The Cashaqua-Rhinestreet contact is considered a muted expression of the well documented *punctata* event in North America (Lash, 2019). Magnetic susceptibility readings published by Lash (2019) show the ^{13}C excursion in this locality begins at 40 cm below the contact, where the excursion has its final peak. At 10 cm below the Cashaqua-Rhinestreet contact, the ^{13}C excursion peaks, and the number of suspected species sampled drops from 22 at 10 cm below to 11 (50% reduction) at the contact; the number of genera drops from the Cashaqua's highest of 18 (at 10 cm below the contact) to 10 at the contact. The value of N$_{species}$ remains low, ranging from 5–17 species (genera count of 5 to 14), throughout the entirety of the Rhinestreet. The lowest number of genera within the Rhinestreet, a notable second plummet, occurs at 60 cm above the contact. The reduction of genera occurs where the lithology shifts to a well lithified black shale that took the longest to disaggregate (14 days rather than the 7-day average). From this height in the bed (60 cm) and up to the Scraggy Bed and transition zone of the Rhinestreet-Angola, there is a slow diversity recovery through the ~12 m of well laminated and monotonous shale. Within the Angola Shale foraminiferal populations, the richness and diversity are essentially consistent (genera = 16 to 18 and suspected species within those genera = 20 to 25); there was no statistically significant increase in diversity, richness, or abundances. However, there was a peak in the number of genera (17) and the suspected species (26) within the Pipe Creek member which lays in contrast to the literature.

The Pipe Creek bed marks the onset of the Lower Kellwasser Event and contains the highest N$_{species}$ count of all beds sampled. The Pipe Creek bed is flanked by gray shales (the Angola and Hanover Members) and shows periodic increases (~10–18%) in epifaunal and mixed populations. These characteristics suggest that within the time just prior to, during, and immediately after the Lower Kellwasser Event this portion of the deltaic complex was either well oxygenated or the organic influx remained high and there was essentially no major biotic turnover; genera/species remain the same, abundance, diversity, and richness are statistically unchanged within the Pipe Creek Shale. Up-section, the

Hanover Shale contains a continuously diminishing number of genera. While this may be reflective of a biotic crisis event, our sampling did not extend high enough within the member to determine whether this is the case. Within the reaches of this investigation, particularly for the foraminiferal assemblages of the Hanover Shale, the potential expression of a biocrisis event in foraminifera may not be as distinct as in the macrofaunal community due to the opportunistic nature of the foraminiferal populations in these deltaic environments and the lack of taxonomic literature with which to identify species (thus muting any changes in diversity).

CONCLUSIONS

The Late Devonian (Frasnian) shales of western New York contain distinct benthic foraminiferal assemblages that are reflective of a shallow environment most likely below storm wave base, as previously suggested (Vogel et al., 1987). The foraminiferal biofacies found within these beds, *Ammobaculites* and *Saccammina* in particular, are in agreement with well-established Cenozoic and Mesozoic biofacies and suggest that the use of predominance facies analysis (Poag, 1981) and benthic foraminiferal depth zonation (Culver, 1988) may work well into the Paleozoic Era; a more thorough investigation of the sedimentary units in western New York may assist in better constraining water depth. The deep infaunal taxa that dominate black shale formations also dominate gray shale formations which suggests that oxygen conditions within the uppermost sediment were possibly hypoxic. Shale units marking or straddling known and confirmed marine crisis events (e.g., *punctata*, Lower Kellwasser) have a muted expression within the Appalachian Basin's Catskill deltaic wedge. This expression may not be as distinct as the coeval macrofaunal populations due to the opportunistic nature of the populations. Foraminifera, though diminutive in size, are abundant within the shale members of the Appalachian Basin in western New York and offer unique insights into paleoecological conditions of basins where ecological conditions are still disputed and may serve as a useful biostratigraphic tool where others have failed. A thorough examination of species within the Appalachian Basin would better constrain these populations and offer more clarity into species-level extinctions throughout the marine crises event.

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